

BEHAVIOR ANALYSIS AND REVALUATION

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Revaluation refers to phenomena in which the strength of an operant is altered by reinforcer-related manipulations that take place outside the conditioning situation in which the operant was selected. As an example, if lever pressing is acquired using food as a reinforcer and food is later paired with an aversive stimulus, the frequency of lever pressing decreases when subsequently tested. Associationist psychology infers from such findings that conditioning produces a response–outcome (i.e., reinforcer) association and that the operant decreased in strength because pairing the reinforcer with the aversive stimulus changed the value of the outcome. Here, we present an approach to the interpretation of these and related findings that employs neural network simulations grounded in the experimental analysis of behavior and neuroscience. In so doing, we address some general issues regarding the relations among behavior analysis, neuroscience, and associationism.

Key words: associationism, devaluation, neural network, respondent feedback, revaluation, simulation

This article has two main purposes: (a) to characterize phenomena that are conventionally grouped under the heading of *revaluation* and (b) to propose an approach toward interpreting these phenomena that is consistent with biobehavioral principles—that is, principles based upon the experimental analysis of behavior and neuroscience (cf. Donahoe & Palmer, 1989, 1994). Revaluation has important implications for both experimental and applied behavior analysis, and its interpretation has been posed as a challenge to a biobehavioral approach (Williams, 1997).

Revaluation

Revaluation refers to phenomena in which the strength of an operant changes by virtue of manipulations that are applied to the reinforcer *outside* the conditioning procedure that selected the operant. As an example (Colwill & Rescorla, 1985; see also Holland & Rescorla, 1975), rats acquired a lever-pressing response, which was maintained with food pellets as the reinforcer, delivered according to a variable-interval (VI) schedule. Following conditioning, food pellets were delivered in the same test chamber but with the lever inaccessible. Immediately thereafter, the animals were injected with lithium chloride (LiCl). Lithium chloride is a nausea-inducing toxin that conditions a taste aversion to the food with which it is paired (Garcia, Kovner, & Green, 1970). On the day after taste-aversion training, the animals were returned to the test chamber, but the lever was again accessible. The critical finding was that the rate of lever pressing declined even though lever pressing had previously been followed only by food pellets, not LiCl. Moreover, the weakening of lever pressing was not due to an indiscriminate suppression of all activity by the toxin. Concurrently with lever pressing, a second operant—chain pulling—had been reinforced on the same VI schedule but with a different reinforcing stimulus—sucrose liquid. If the pellet–toxin pairing had exerted its effect on lever pressing via competition from nausea responses conditioned to the experimental context, then chain pulling should have been weakened as much as lever pressing. (In the

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actual experiment, the particular operant that was followed by the reinforcer and the particular reinforcer that was paired with the toxin were counterbalanced across subjects.) Thus, the effects of the devaluation procedure were relatively specific to the operant whose reinforcer had been paired with the aversive stimulus. Further work has identified a number of additional extraconditioning manipulations that can alter the strength of an operant, such as exposure to the reinforcer at a different deprivation level (for reviews, see Balleine & Dickinson, 1998; Colwill, 1993, 1994; Delamater & LoLordo, 1991; Dickinson, 1997; Macintosh & Dickinson, 1979; Rescorla, 1998).

Revaluation is the more general term for the effects of extraconditioning manipulations on the strength of responding; *devaluation* is reserved for those instances in which the response weakens. We employ revaluation simply as a collective term under which to group extraconditioning reinforcer-related manipulations that affect conditioned responding. Within the literature in which it has been described and discussed, however, revaluation more typically connotes a particular theoretical stance toward the interpretation of these effects—associationism. The associationist approach has been described as follows:

The single theoretical term which is central to explanations . . . of learning is the association. Theories of animal learning attempt to represent virtually all of the learning of relations in terms of the formation of an association between two elements. . . . The notion of association which they employ differs little from that described in the 19th century by British philosophers. (Rescorla, 1985, p. 39)

Or, stated more succinctly, "Behavior is but a spade to disinter thought" (Dickinson, 1979, p. 553).

We have found one technique particularly valuable for exposing the range of associations. . . . Animals are given the opportunity to form an association between the elements of interest. Then one of those elements is endowed with a new property, perhaps the ability to evoke some response. Then the animal's behavior to the other element is tested; to the extent that it too has that new property, we infer the formation of an association between the elements. (Rescorla, 1985, p. 48)

As stated, behavioral observations serve as the basis for *inferences* about underlying entities of

which behavior is assumed to be the expression. In the prior example of devaluation, an operant contingency between lever pressing and food pellets was inferred to produce a response–outcome association. The subsequent pairing of pellets with LiCl was inferred to devalue the outcome, thereby altering one constituent of the response–outcome association and weakening the operant. (For critical examinations of inferred-process theories, of which associationism and cognitivism are leading examples in psychology, see Hinde, 1992; Marr, 1997; Moore, 1996, 1997; Skinner, 1950; Williams, 1986; and also Donahoe & Palmer, 1989, 1994, p. 29; Palmer & Donahoe, 1992.)

A science of behavior must ultimately accommodate all reliable functional relations between the environment and behavior, most especially those of such potential importance as revaluation. The implications of reinforcer revaluation for both basic and applied behavior analysis are considerable: Manipulations applied solely to the reinforcer may change the strength of the operant. In short, revaluation appears to demonstrate that the effects of a three-term contingency can be altered by procedures that do not involve the middle term (the operant), but only a two-term contingency between the reinforcer and other events. Revaluation encompasses an important set of phenomena, but associations cannot provide a basis for interpreting them in behavior analysis (Donahoe, 1999). Associations are inferred processes and, as such, cannot be manipulated or measured. That is, they are not subject to direct experimental analysis (cf. Skinner, 1966). Associationism makes use of a conceptual approach that Skinner (1938, 1950) labeled a *conceptual nervous system* and, as such, is particularly susceptible to the twin temptations of the nominal fallacy and logical circularity (Skinner, 1957; see also Donahoe & Palmer, 1989, 1994, p. 127).

How, then, are we to proceed when faced with the prospect that existing behavior-analytic principles may not yet provide an interpretation of revaluation? One approach is to seek out environmental and behavioral conditions that are necessary and sufficient for revaluation. These conditions could then be used to define a higher order contingency under which to nest the standard three-term contingency of environment-behavior-rein-

forcer (cf. Sidman, 1986). In short, the higher order contingency would specify establishing operations for the revaluation of operants (Keller & Schoenfeld, 1950; Michael, 1982, 1993; cf. Fischer, Iwata, & Worsdell, 1997). Interpretation via establishing operations meets the covering law criterion of scientific explanation because, if such conditions can be identified, they would distinguish the circumstances in which revaluation occurs from those in which it does not (Hempel, 1965). In addition, a higher order contingency might suggest further experimental analyses that would uncover new behavioral processes. Whether a comprehensive set of establishing operations can be identified for revaluation is an empirical matter that remains to be adjudicated by experimental evidence. A generic set of establishing operations would avoid what Skinner (1938) called the "botanizing of reflexes."

The number of stimuli to which a[n organism] may come to respond . . . is indefinitely large, and to each of them it may be made to respond in many ways. It follows that the number of possible reflexes is for all practical purposes infinite and that what one might call the botanizing of reflexes will be a thankless task . . . and has no further theoretical interest. (pp. 10, 11, 12)

An alternative strategy that is also consistent with behavior analysis is to supplement behavioral principles with the fruits of experimental analyses conducted at other scales of measurement, such as those of neuroscience. In the course of explanation in science generally, when the explanatory variance of variables defined at one scale of measurement has been exhausted, order is sought by introducing variables defined at neighboring scales. Interpretations of behavior that incorporate neuroscience were explicitly and consistently endorsed by Skinner. "The experimental analysis of behavior is a rigorous, extensive, and rapidly advancing branch of biology" (Skinner, 1974, p. 255).

The physiologist of the future will tell us all that can be known about what is happening inside the behaving organism. His account will be an important advance over a behavioral analysis, because the latter is necessarily "historical"—that is to say, it is confined to functional relations showing temporal gaps. (Skinner, 1974, pp. 236–237)

And again,

A behavioral analysis has two necessary but unfortunate gaps—the spatial gap between behavior and the variables of which it is a function and the temporal gap between the actions performed by the organism and the often deferred changes in its behavior. These gaps can be filled only by neuroscience, and the sooner they are filled, the better. (Skinner, 1988, p. 470; see also Skinner, 1938, p. 448)

When Skinner first made such comments, much remained to be discovered at the behavioral scale of measurement, and most of the relevant neuroscience was also a task for the future. The situation is quite different now. The science of behavior is becoming a mature discipline, and neuroscience is increasingly competent to fill the "temporal gaps" (see Donahoe, 1996; Michael, 1998).

In the remainder of this article, we explore a biobehavioral approach to interpreting revaluation (Donahoe & Palmer, 1994). The biobehavioral approach differs chiefly from inferred-process accounts in that the gap-filling events are products of *independent* experimental analyses, not inferences from behavioral observations alone (Moore, 1997; cf. Anderson, 1978; Hintzman, 1993; Roediger, 1990; Watkins, 1990).

Biobehavioral Interpretation of Revaluation

To interpret revaluation, we used artificial neural networks. An artificial neural network is a set of interconnected units that simulate neurons (or groups of neurons) whose strengths of connections (i.e., connection weights) simulate synaptic efficacies. An artificial neural network need not incorporate all potentially relevant information from neuroscience, only the minimally necessary constraining and enabling features to accommodate the behavioral relations being simulated. In interpretation, as in experimental analysis, new variables are introduced only until order emerges (cf. Skinner, 1950). Although simulations using artificial neural networks need not incorporate all potentially relevant findings, nothing in the simulation should be inconsistent with experimental analysis. In short, artificial neural networks are constrained by a subset of the relevant biobehavioral principles, precisely the subset that permits the phenomena of interest to be simulated. As the simulated phenomena be-

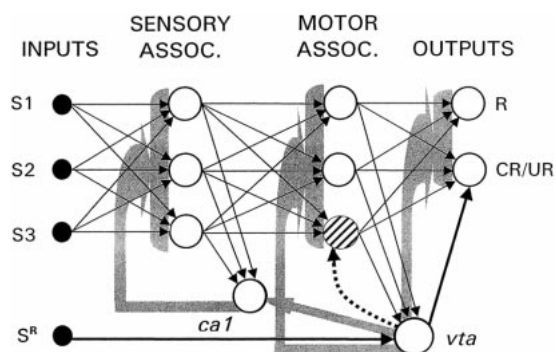


Fig. 1. Architecture of the neural network used to simulate the effects of reinforcement on the selection of environment-behavior relations. Stimulation of input units (e.g., S1) simulates the occurrence of stimuli with the S^R unit reserved for the reinforcing stimulus. Stimulating the input units initiates activity in the processing units—sensory- and motor-association units and output units. Stimulating the S^R input unit activates the diffusely projecting reinforcement system (indicated by the two rightmost gray regions) originating in the simulated ventral tegmental area (*vta*). The reinforcement system modifies the strengths of connections to motor-association and output units, and modulates the activity originating in the *ca1* region of the simulated hippocampus. The diffusely projecting hippocampal system (indicated by the leftmost gray region) modifies the strengths of connections to sensory-association units. Straight lines with arrows indicate feed-forward connections that lead ultimately to output units simulating the behavior of the network—the operant (R) unit and respondent (CR/UR) unit. The broken arc indicates a feedback connection from the *vta* unit of the reinforcing system to a motor-association unit. The motor-association unit that receives reinforcer feedback is crosshatched.

come more complex, the need to incorporate additional information may increase (Donahoe, 1997).

The structure (architecture) of the artificial neural network used to interpret revaluation is shown in Figure 1. On the left side are input units understood as activated by stimuli from the environment of the network. Units S1, S2, and S3 are activated by arbitrary stimuli; Unit S^R is activated by stimuli that function as reinforcers. Diffuse projections from CA1 neurons of the hippocampus modify synaptic efficacies from sensory to sensory-association neurons. This diffusely projecting system is simulated by the leftmost gray region arising from *ca1*. Sensory-association units are connected to motor-association units, and these units are, in turn, connected to output units. Activation of the R output unit simulates the operant. Activation of the

CR/UR output unit simulates the responses evoked by the reinforcer (S^R). Synaptic efficacies from sensory- to motor-association units and from motor-association to output units are modified by a second diffusely projecting system from the ventral tegmental area (VTA) of the midbrain, which is activated by the S^R unit. The diffusely projecting midbrain reinforcing system is simulated by the two gray regions that arise from the *vta* unit. The connection from *vta* to *ca1* allows stimulation of the S^R unit to modulate the diffuse output of *ca1* to sensory-association units. By this means, reinforcers coordinate perceptual learning with motor learning (Donahoe & Palmer, 1994, pp. 196–199).

The architecture of the artificial neural network is consistent with neuroanatomical findings regarding the diffusely projecting systems from the VTA to motor-association cortex and from CA1 to sensory-association cortex (see Donahoe, 1997; Donahoe, Burgos, & Palmer, 1993; Donahoe & Palmer, 1994). The learning algorithm that modifies connection weights between units is consistent with neuroscientific research on long-lasting long-term potentiation (LTP) (Frey, 1997; see also Bliss & Lømo, 1973; Frey, Huang, & Kandel, 1993; Stein, Xue, & Bel-luzzi, 1993) and yields emergent effects that are consistent with behavioral principles of conditioning (Donahoe et al., 1993; Donahoe, Crowley, Millard, & Stickney, 1982). Long-term potentiation is a process whereby coactivity between neurons in synaptic contact is necessary for long-lasting increases in the ability of a presynaptic neuron to activate a postsynaptic neuron. Coactivity produces long-lasting increases in synaptic efficacies only if a neuromodulator (e.g., dopamine) is concurrently introduced into the synapse due to the occurrence of a reinforcing stimulus. Coactivity in the absence of the neuromodulator produces long-lasting decreases in synaptic efficacies—so-called long-term depression (Wickens & Köster, 1995). Long-term potentiation is a ubiquitous process that has been found in many regions of the brain including sensory cortex (Bear, 1996), motor cortex (Hess & Donoghue, 1996), and subcortical structures (Maren, 1996) as well as CA1 hippocampal neurons where the neural circuitry permits it to be most readily studied. When the learning algorithm is implemented

within the foregoing network architecture, aspects of a number of behavioral phenomena have been simulated, including acquisition, extinction, reacquisition, inter- and intradimensional discrimination, temporal discrimination, stimulus generalization, blocking, and conditioned reinforcement with both Pavlovian and operant procedures (Burgos, 1996, 1997; Burgos & Donahoe, in press; Donahoe, 1997; Donahoe & Burgos, 1999; Donahoe & Palmer, 1989, 1994; Donahoe et al., 1993; Donahoe, Palmer, & Burgos, 1997).

The network functioned as follows with an operant contingency. Stimulation of one or more input units simulated the occurrence of environmental stimuli. These stimuli could include phasic stimuli controlled by the experimenter as well as tonic, or contextual, stimuli such as the sight of the operandum (cf. Donahoe et al., 1997). (In all present simulations, the environment stimulated only the S1 input unit.) Stimulation of an input unit could activate units "deeper" in the network including, possibly, the operant (R) unit (e.g., lever pressing). If the R unit was activated, the computer program stimulated the reinforcer input unit (S^R) (e.g., by the presentation of food). When the S^R unit was stimulated, the diffusely projecting *vta* reinforcing system simulated the liberation of a neuromodulator, which caused connection weights to increase between all recently coactive units. In addition, stimulation of the S^R unit unconditionally activated the CR/UR unit, simulating the respondents elicited by the reinforcer. With reinforced training, connection weights increased along pathways that permitted the environment to control both the operant (R unit) and the respondent (CR/UR unit).

A biobehavioral interpretation of reevaluation exploits a feedback connection from units in the reinforcing system to one or more motor-association units (see Donahoe & Palmer, 1994, pp. 108–109). (Technically, such connections are recurrent connections in that they permit the activity of a unit to be affected by its own prior activity; cf. Hutchison, 1997.) In Figure 1, the feedback connection is indicated by the dashed arrow extending from the *vta* unit to the crosshatched motor-association unit. Hereafter, a motor-association unit that receives a recurrent connection from the *vta* is called a *feedback unit*

because its state of activation is affected, in part, by the activation of units in the reinforcing system. (We have conducted simulations, not reported here, in which feedback units received recurrent connections from the CR/UR unit, a more "peripheral" form of feedback. The results were qualitatively indistinguishable from those described here.) Feedback connections are well documented throughout the brain. In the reinforcing system of the midbrain, projections from the VTA to the neostriatum—where efferents from sensory systems converge on afferents to motor systems—are complemented by projections back to the midbrain (e.g., Groves et al., 1995; Wickens & Kötter, 1995). Recurrent connections are present in both cortical and subcortical regions (Fuster, 1989, 1995). Most pertinent to reevaluation, recent observations indicate that reevaluation is prevented by damage to the region of the motor-association cortex that is the target of the feedback connections simulated here (i.e., neurons in prefrontal cortex) (Gallagher, McMahan, & Schoenbaum, 1999; see also Watanabe, 1998).

The process whereby motor-association units that received reinforcer feedback came to influence the activation of the R unit was as follows: Early in operant conditioning, the R unit was only weakly activated by its inputs from motor-association units because connection weights along these pathways were relatively small; that is, the operant was emitted. Connection weights, w , varied between zero and one, $0 < w < 1$, and were assigned a value of .01 at the outset of the simulations. When the R unit was activated on the penultimate time-step of the simulation, the S^R unit was stimulated, which caused the *vta* unit (i.e., the reinforcing system) and CR/UR unit (the respondent) to become strongly activated. The simulations were discrete-time simulations in which connection weights were updated on five time-steps within each trial. The time interval between trials was assumed to be long enough to permit the activations of units to decay to their spontaneous levels of no more than .007 before the beginning of the next trial. Connection weights between units along the S^R -*vta*-CR/UR pathway were large from the outset of conditioning because these pathways permitted the environment to elicit the respondent. Motor-association units

that are targets of feedback pathways from units within the reinforcing system have the potential to become activated via such pathways. Because feedback motor-association units were activated by these pathways, connection weights to them from units activated by environmental stimulation, and from them to the R unit, disproportionately increased relative to the connection weights to other motor-association units that did not receive feedback. Feedback units were activated by inputs from both the environment and the reinforcer system, whereas other motor-association units were activated by inputs from environmental stimulation alone. The net effect of this difference between the activation of feedback units and other motor-association units was that pathways from the S1 to the R unit that included feedback units played a larger role in mediating the operant than pathways devoid of such units. (Other factors amplified this effect, but are not considered here; see Donahoe & Palmer, 1994, p. 60.) In short, the operant came under the joint control of the environment and reinforcer feedback instigated by the environment.

Simulation of operant conditioning with reinforcer feedback. Figure 2 illustrates the effect on the strength of the operant of feedback from the reinforcing system. (The values of all parameters in the neural network simulations were identical to those used in previous work; e.g., Donahoe et al., 1993.) The activation levels during the first 125 trials of acquisition are shown for three units: the operant unit (R), the respondent unit (CR/UR), and the motor-association unit receiving reinforcer feedback. Figure 2 shows independent replications of four simulations to give a sense of variations in the outcome. First, consider changes in the activation of the R and CR/UR units. With an operant contingency, the presence of a simulated environmental stimulus (S1) initially allowed the R unit to be activated at a level slightly greater than zero. This caused the S^R unit to be stimulated according to the operant contingency. The S^R unit then activated the reinforcing system, which changed connection weights between all recently coactive units. Over successive reinforcers, connection weights increased along pathways from S1 to R and from S1 to CR/UR. In terms of a behavioral experiment, the sight of the lever (S1) occasioned both lever

pressing (R) and salivation (CR) (cf. Skinner, 1935, p. 67). Stimulation of S1 activated the CR/UR unit earlier in the conditioning process than the R unit (see Figure 2), because units along the respondent pathway were strongly activated from the outset of conditioning. Accordingly, connections from environmental inputs to units along respondent pathways increased more rapidly. The more rapid changes in connection weights along S1-CR pathways than S1-R pathways are not externally imposed on the simulation, but emerge as a consequence of the biologically informed learning algorithm: From what is known about LTP, synaptic efficacies increase more rapidly between more strongly coactive neurons (e.g., Frey, 1997; see also Donahoe, 1997). (The present account of revaluation is not dependent on the more rapid emergence of the CR than the R as detected at the behavioral scale of measurement. It is dependent on the more rapid increase in synaptic efficacies between units along the S1-CR pathways that mediate the respondent than along pathways that mediate the operant. The behavioral consequences of unit activity along S1-CR pathways vary with the particular conditioning preparation and can be affected by a number of factors, such as interactions between respondent and operant behavior; cf. Donahoe & Palmer, 1994, pp. 51–52.)

For present purposes, the most pertinent changes are those that involve the motor-association unit receiving feedback from the reinforcer system. The activation of the feedback unit is shown in Figure 2, which indicates that the feedback unit became strongly activated later in conditioning than the CR unit but *before* the R unit. Thus, the feedback unit was activated early enough during acquisition for the reinforcer disproportionately to strengthen pathways from the feedback unit to the operant unit. Again, this sequence of events is not imposed extrinsically, but emerges from the action of the learning algorithm on connection weights within the network. The net effect is that activation of the R unit became jointly dependent on stimulation from S1 and reinforcer feedback. The environment retains ultimate control of the operant, however, because reinforcer feedback is itself instigated by the environment. Neural networks that implement reinforcer feedback are no more autono-

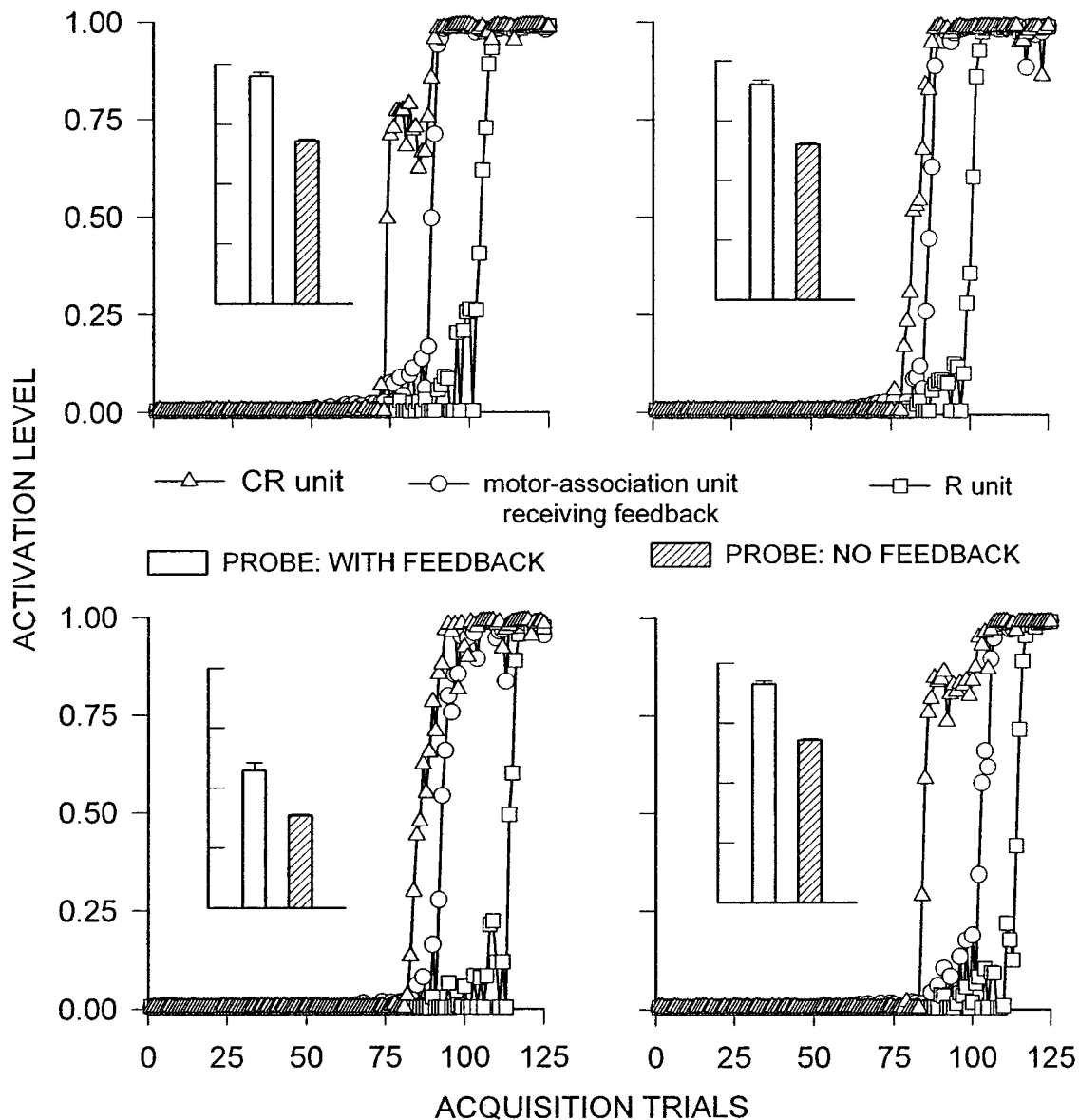


Fig. 2. Simulation results with an operant contingency during acquisition and during probe tests conducted after acquisition. Each panel shows an independent replication of acquisition and probe testing. The line graphs within each panel depict the activation levels for the operant (R) unit and respondent (CR/UR) unit during the first 125 trials of acquisition, and for the motor-association unit that received feedback from the reinforcer system. The bar graphs within each panel depict the mean activation level of the operant unit during 50 probe tests. The open bar indicates operant responding when the motor-association unit received reinforcer feedback; the cross-hatched bar indicates operant responding when reinforcer feedback was reduced (see text). Error bars indicate the standard error of the mean activation during 50 probe tests. The maximum activation level was 1.0 for all graphs.

mous than the organisms whose behavior they are intended to simulate.

Reinforcer feedback and devaluation. If operants are under the joint control of environmental stimuli and reinforcer feedback, then

any extraconditioning manipulation that alters feedback will alter the strength of the operant. Altering the activation of feedback units changes the strength of the S1-R relation because these motor-association units

disproportionately contribute to the S1-R environment-behavior relation. To assess the contribution of reinforcer feedback to operant responding, 50 probe tests were conducted. In probe tests, the network functioned as usual except that any changes in connection weights that would otherwise have been produced by extinction were precluded. Probe tests were conducted under two conditions, one with reinforcer feedback remaining at postconditioning levels and one with the connection weight of the feedback pathway reset to its initial value prior to conditioning (i.e., .01). Resetting the connection weight of the feedback pathway simulated the effects of any biobehavioral process that reduced reinforcer feedback. The leftmost bar of the bar graphs contained within each of the panels of Figure 2 indicates that S1 strongly activated the R unit during the probe tests when feedback was present. However, when reinforcer feedback was reduced by resetting the weight of the feedback connection, the activation of the R unit decreased. This decrease in operant strength is shown by the rightmost bar within each panel. Although the decline in operant strength varied somewhat from simulation to simulation, reductions in reinforcer feedback invariably decreased operant responding. Thus, any biobehavioral process that decreases reinforcer feedback will produce devaluation.

The foregoing simulations indicate that reductions in reinforcer feedback are sufficient to alter the strength of an operant. However, simulation of the specific biobehavioral processes that are recruited by revaluation procedures remains a task for the future. If simulations are to provide a fully adequate scientific interpretation, and not merely an appeal to a conceptual nervous system, they must be informed and constrained by additional information from experimental analysis. In particular, they must identify specific means by which the reinforcing system (or neurons activated by the reinforcing system) interacts with the neural processes recruited during revaluation procedures. A number of promising candidates exist. As an example, it is known that particular regions of the amygdala are involved in taste aversions, that the amygdala has connections with the ventral tegmental area as well as other regions of the brain, and that stimulation of portions of the

amygdala evoke motor activity that results in escape behavior (e.g., Bielavska & Roldan, 1996; DeOca, DeCola, Maren, & Fanselow, 1998; Han, McMahan, Holland, & Gallagher, 1997; Hatfield, Han, Conley, Gallagher, & Holland, 1996; Yamamoto, Shimura, Sako, Yasoshima, & Sakai, 1994; see also Donahoe & Palmer, 1994, p. 115, and Holland, 1997). Thus, opportunities exist for interactions between the systems mediating taste aversions and operants at both the neural and behavioral levels.

Amount of reinforcer feedback and devaluation. In associationist accounts of revaluation, the level of operant responding is inferred to reflect the net effect of various types of associations—stimulus-response and response-outcome associations as well as so-called hierarchical associations between stimuli and response-outcome associations, that is, S-(R-O) associations. To the extent that operant responding reflects R-O and S-(R-O) associations, the environment cannot occasion the operant if the outcome has been completely devalued (Colwill & Rescorla, 1990a; but see also Colwill, 1993). Although various experimental procedures have apparently completely devalued the reinforcing stimulus (i.e., the reinforcer was no longer ingested after pairing with LiCl) “no experiment on reinforcer devaluation has succeeded in completely eliminating the operant response” (Mazur, 1994, p. 182; see also Colwill & Rescorla, 1988, 1990b). The following simulations of reinforcer feedback provide an interpretation of the process whereby the magnitude of revaluation can vary in different circumstances.

These simulations used an artificial neural network of the same general architecture as shown in Figure 1, but increased the number of units in the sensory- and motor-association regions from three to five. This change permitted the number of motor-association units receiving feedback to increase from one to three, while the number of motor-association units that did not receive feedback was held constant at two. During 125 trials of operant conditioning, stimulation of the S1 unit became able to activate the operant (R) unit. However, as in earlier simulations, operant responding was acquired only after S1 had acquired control over the respondent (CR/UR) unit and, thereby, the feedback units. (Figure 3 depicts the activations of only one of the

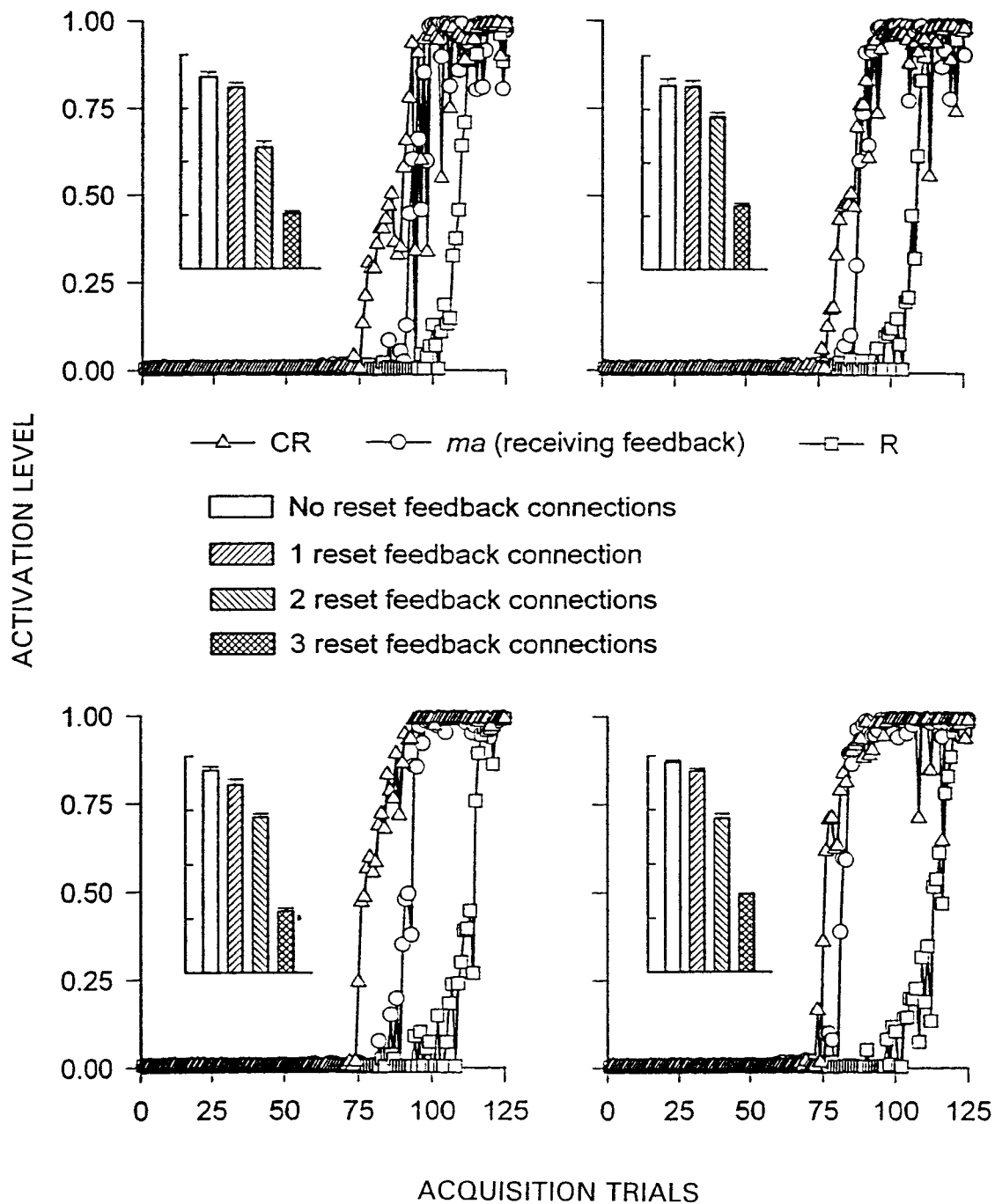


Fig. 3. Simulation results with an operant contingency during acquisition and during probe tests conducted after acquisition. Each panel shows an independent replication of acquisition and probe testing. The line graphs within each panel depict the activation levels for the operant (R) unit and respondent (CR/UR) unit during the first 125 trials of acquisition, and for one of three motor-association (*ma*) units that received feedback from the reinforcer system. The bar graphs within each panel depict the mean activation level of the operant unit during 50 probe tests. The open bar indicates operant responding when all three motor-association units received reinforcer feedback. The crosshatched bars indicate operant responding when reinforcer feedback was progressively reduced (see text). Error bars indicate the standard error of the mean activation during 50 probe tests. The maximum activation level was 1.0 for all graphs.

three feedback units, but similar findings were obtained for the other two units.) Probe tests conducted following conditioning indicated that activation of the R unit by the environment was heavily dependent on pathways that contained feedback units. The leftmost bar in each of the bar graphs shows that the operant unit was highly activated when the connection weights between the *vta* unit and all three feedback units remained as they were at the end of conditioning. However, the strength of the operant progressively declined as connection weights to increasing numbers of feedback units from the reinforcing system were reset to their values prior to conditioning. Thus, increased opportunities for reinforcer feedback during original conditioning increased the effect of subsequent devaluation. Weakening—even eliminating—an operant by a devaluation procedure does not force the inference of either R-O or hierarchical S-(R-O) associations. Variations in the effectiveness of devaluation procedures can reflect differences in the *quantity* of reinforcer feedback controlled by the environment, not the *quality* of associations. The three-term contingency remains the central insight, whatever the magnitude of devaluation effects.

Revaluation through changes in deprivation level or reinforcer magnitude. To the degree that reinforcer feedback partially controls an operant, any extraconditioning procedure that alters reinforcer feedback changes the strength of the operant. Heretofore, we have considered only procedures that decrease operant responding: devaluation. However, extraconditioning procedures that increase the strength of operants have also been identified (e.g., Balleine, 1992; Dickinson & Dawson, 1988). From the perspective of a reinforcer-feedback interpretation of revaluation, these findings are not necessarily problematic: Extra-conditioning manipulations that increase the ability of the original training environment to activate feedback units should strengthen the operant. How might this occur?

Revaluation was simulated using the network architecture shown in Figure 1, but the S^R input unit was now stimulated at a level of .5 during operant conditioning instead of 1.0 as in prior simulations. The decrease in activation of the S^R unit simulated reducing the

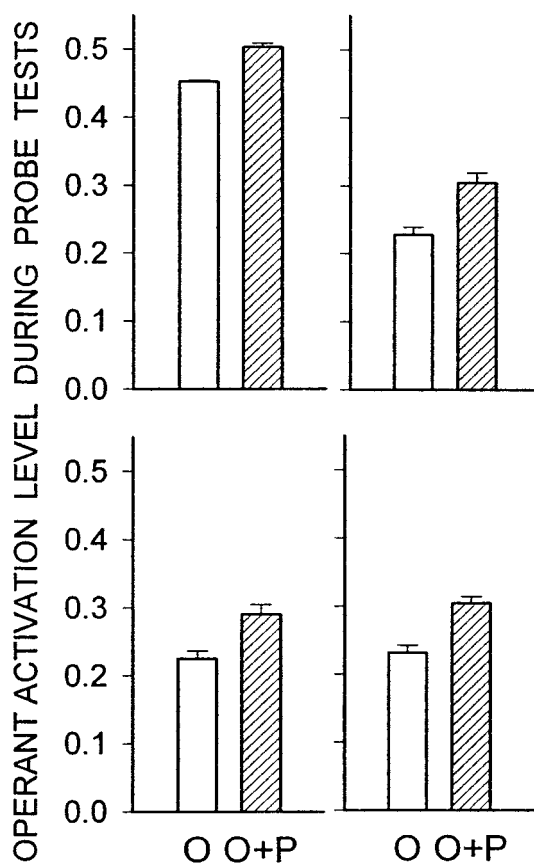


Fig. 4. Simulation findings of operant responding during probe tests conducted after operant training (O) with the S^R unit activated at a level of .5 and after operant training was followed by Pavlovian (i.e., respondent) training (O+P) in which the S^R unit activated at a level of 1.0. Each panel shows an independent replication of operant responding after these two procedures. Error bars indicate the standard error of the mean activation during 50 probe tests.

reinforcer magnitude or reducing the deprivation level relative to earlier simulations. After 200 acquisition trials under the operant contingency, the *same* network was given an additional 200 trials with a two-term ($S1-S^R$) Pavlovian contingency, but the S^R unit was now activated at an increased level of 1.0. This simulates an upward shift in reinforcer magnitude or deprivation level during the Pavlovian procedure. Then, 50 probe tests were given to assess the strength of the operant. Figure 4 shows four independent replications of the simulation. The left bars show the level of activation of R units at the end of operant training. The right bars show the lev-

els of activation of the same R unit on probe trials following Pavlovian conditioning with the more strongly stimulated S^R unit. During these latter probe tests, the connection weights from all motor-association units to the R unit were set to the values they had attained at the end of operant conditioning. This eliminated the possibility of "superstitious" strengthening of the operant during Pavlovian training. As can be seen, the strength of the operant was *increased* by the intervening Pavlovian contingency. The revaluation effect was produced in the following manner: The stronger activation of the S^R unit during the Pavlovian procedure increased connection weights from motor-association units to the *vta* unit and from the *vta* unit to the feedback unit. Then, during probe tests, these increased connection weights permitted the unchanged intensity of stimulation of the S1 input unit to activate the feedback unit more strongly. Because the feedback unit was an important constituent of the pathways leading to the operant unit, the operant unit became more strongly activated. Thus, reinforcer feedback provides a means whereby both decreases (devaluation) and increases (revaluation) in the strength of operant responding may occur.

Conclusions

We have used neural networks to simulate a biobehavioral process—reinforcer feedback—that has the potential to interpret revaluation. (For theoretical proposals that appeal to processes inferred from behavior, see Amsel, 1989; Amsel & Rashotte, 1984, pp. 34–44; Dragoi & Staddon, 1999; Hull, 1930, 1931; Overmier & Lawry, 1979; Rescorla & Solomon, 1967; Trapold & Overmier, 1972; cf. Rescorla & Colwill, 1989.) These simulations demonstrate that extraconditioning procedures that involve only the reinforcer can decrease (Figure 2) or increase (Figure 4) the strength of an operant. The changes occurred when reinforcer feedback decreased or increased, respectively. Moreover, the magnitude of these effects varied with the extent of reinforcer feedback, with revaluation increasing as the opportunity for feedback increased (Figure 3).

We turn now to three phenomena that are related to revaluation, and consider how each can be addressed by the present approach.

Specificity of devaluation. First, consider a finding described when devaluation was introduced at the outset of this theoretical note; namely, devaluation is relatively specific to the particular reinforcer with which the aversive stimulus has been paired (Colwill & Rescorla, 1985). According to a biobehavioral interpretation of revaluation, extraconditioning manipulations affect the strength of an operant if they change reinforcer feedback. Reinforcer feedback changes the strength of the operant, because motor-association units that receive reinforcer feedback disproportionately participate in pathways that mediate the selected environment–behavior relation. Motor-association units that serve as feedback units acquire this function because, unlike other motor-association units, they can be activated by pathways from two sources: (a) Environmental stimuli present during both conditioning and revaluation activate feedback units via pathways from (ultimately) input units, and (b) reinforcing stimuli and environmental stimuli (after conditioning) activate units in the reinforcing system that, in turn, activate feedback units via recurrent connections. In the nervous system, different stimuli (e.g., the sight of a lever vs. the sight of a chain) activate somewhat different sensory neurons, and different operants (e.g., lever pressing vs. chain pulling) involve somewhat different motor neurons. As a result, the motor-association neurons for different operants are different. Any manipulation that differentially affects these motor-association neurons (simulated by feedback units) would differentially affect the strengths of the operants that they mediate.

How may a devaluation procedure (pairing one of the reinforcing stimuli with an aversive stimulus) differentially affect different sets of feedback units? Until this point in the interpretation of revaluation, a reinforcing stimulus has been considered to activate all *vta* units and, thereby, all motor-association units receiving feedback connections. If this were the case, all reinforcers would activate feedback units for all operants via recurrent connections from *vta* units that had been strengthened during conditioning. However, if different reinforcing stimuli activated somewhat different subpopulations of *vta* units within the diffusely projecting reinforcing system, feedback units for different op-

erants would not be identical. Then, interactions of feedback units with the neural systems activated by the aversive stimulus could differentially affect the operant selected by its corresponding reinforcer. During devaluation, those feedback units that mediate the specific operant would be coactive with units activated by the aversive stimulus paired with the reinforcer. Coactivity is necessary for modification of connection weights between neurons and, accordingly, interactions can occur between the neural systems that are activated by the aversive stimulus and the neural systems that mediate the specific operant.

What is the evidence from neuroscience regarding whether different reinforcers do, in fact, activate different neurons in the reinforcing system? The evidence is supportive. Taste receptors in the tongue project to neurons in the solitary nucleus of the midbrain and, from there, to neurons in the VTA (among others). Neurons in the solitary nucleus respond differentially to the four basic tastes (salt, sweet, bitter, and sour; e.g., Smith, Liu, & Vogt, 1996). These neurons then project to neurons in the reinforcing system and motor-association area (among others) where they evoke differential neural responses (e.g., Delfs, Zhu, Druhan, & Aston-Jones, 1998; Rolls, 1997; Schoenbaum, Chiba, & Gallagher, 1998). Thus, independent experimental evidence indicates that pairing the reinforcing stimulus for one operant with an aversive stimulus could differentially affect the reinforcer feedback for that operant. Additional experimental research is needed, but a reinforcer-feedback interpretation of the reinforcer-specific effects of devaluation is consistent with evidence at both the behavioral and neural scales of measurement. This interpretation implies that revaluation should be restricted to the environments common to original conditioning and revaluation. Only these environments would activate the VTA units and motor-association units that are specific to the operant. Behavioral research is consistent with this prediction; revaluation effects are context specific (e.g., Colwill & Rescorla, 1985).

Persistence of devaluation. A second class of revaluation-related phenomena can also be interpreted from a biobehavioral perspective: The effect of devaluation procedures persists

after the operant selected by the reinforcer has been extinguished. The persisting effect of devaluation has been demonstrated using postextinction procedures such as transfer tests (Rescorla, 1996a, 1996b; for a review, see Rescorla, 1998). Persistence is predicted by a reinforcer-feedback account. The strengthened connections between feedback units and the output units that control the operant are relatively deep within the network. We have shown in previous simulation research that connection weights in deeper layers of a network are relatively unchanged by extinction. Deeper connection weights remain intact because repeated stimulation of input units by the conditioning environment during extinction weakens connection weights from input units to sensory-association units. Once these connection weights have been sufficiently weakened, downstream motor-association units that are connected to sensory-association units are no longer activated by the environment. Because units must be coactive for the connection weight between them to change, the connection weights between units deeper in the network do not weaken further. These relatively intact connection weights are then able to affect subsequent performance, as we have shown in simulations of the more rapid reacquisition of an operant following its extinction (Donahoe et al., 1993; Donahoe & Palmer, 1994, pp. 93–95; see also Kehoe, 1989).

Extinction and devaluation. A third class of devaluation-related phenomena is especially interesting because associationist and reinforcer-feedback accounts differ in their predictions, and the data track the latter account. Specifically, associationist theory predicts that extinction of a conditioned response to one of two conditioned stimuli (CSs) would weaken the conditioned response to the other CS if both had individually been paired with the same reinforcer. This prediction is based on the inference that conditioning not only produces interevent associations but also builds up “representations” of the CS and unconditioned stimulus (US) (Rescorla & Heth, 1975, p. 95). If extinction of one CS devalues the “internal memorial representation” of the reinforcer (the US), then CRs should weaken to both of the CSs established with that reinforcer. This should occur because, by definition, an asso-

ciation requires at least two terms, and if one of them—the representation of the US—is weakened, then any behavior that is inferred to reflect an association with the US must also weaken. Contrary to associationist theory, experimental work with both respondent and operant procedures does not support this prediction. Extinction of a CR to one CS does not reduce the CR to a different CS (e.g., Richards & Sargent, 1983), and extinction of one discriminated operant does not reduce the strength of a different operant (Moore, 1986) even when both were selected by the same reinforcer.

By contrast, a reinforcer-feedback interpretation of devaluation predicts that the extinction of one conditioned operant (or respondent) should *not* weaken a second environment–behavior relation selected by that same reinforcer. Extinction reduces connection weights only from input units activated by prevailing discriminative stimuli (or CSs) to other units within the network—notably, motor-association units activated by recurrent connections. Connection weights along pathways that are activated by other discriminative stimuli should not be affected. According to the biologically based learning algorithm, only connection weights between coactive units weaken in the absence of reinforcement. Therefore, reductions in connection weights are specific to the pathways activated by the discriminative stimuli present during extinction. Extinction of an operant in the presence of its discriminative stimulus should not weaken the control of another operant by a different discriminative stimulus. Thus, a biobehavioral account is consistent with the experimental evidence in indicating that extinction need not affect responding to other discriminative stimuli.

The differing accounts of extinction provided by the reinforcer-feedback and associationist approaches also have implications for the effects of revaluation procedures on performance during chain schedules. In one experiment, responding by pigeons was reinforced on a two-component concurrent schedule in which each component consisted of a three-element chain schedule (Williams, Ploog, & Bell, 1995). In an attempt to devalue earlier links of one chain, responding was extinguished during the terminal-link stimulus. However, inconsistent with a multielement as-

sociationist account of chain schedules in which responding during earlier links is maintained by an indirect association with the US representation, responses during earlier links of the chain were *not* differentially weakened. A reinforcer-feedback interpretation of chain schedules does not predict that extinction of responding during the terminal link should affect performance during earlier links: The reinforcers for responding during earlier links are the conditioned reinforcers occasioned by stimuli of the following link, not the unconditioned reinforcer of food that selected responding during the terminal link (Williams & Fantino, 1978; see also Colton & Moore, 1997; Moore, 1986; Williams, 1999). The neural pathways enabling conditioned reinforcement extend from motor-association units activated by that link's discriminative stimulus to the VTA (Donahoe & Palmer, 1994, pp. 96–99). These pathways are not the same for discriminated stimuli of different links and are not the same as those activated by the unconditioned reinforcer (see Figure 1). Thus, weakening the connections activated by the stimulus of the terminal link should not weaken the connections implementing conditioned reinforcement for the other links. Experimental evidence supports the contention that the neural pathways of conditioned and unconditioned reinforcement differ (Donahoe, 1997; Holland, 1997; see also Delamater, 1997; Holland & Rescorla, 1975; Malkova, Gaffan, & Murray, 1997; Watanabe, 1998).

Biobehavioral analysis and associationist psychology. Behavior analysis has resisted efforts to explain environment–behavior relations through appeals to inferred processes, such as associations, that are wholly inferences from behavior. It is thought better to acknowledge whatever difficulties may confront a purely behavioral analysis than to camouflage those difficulties by appeals to inferred processes. This strategy has proven effective. Behavior analysis has largely avoided the conceptual problems that plague inferred-process theories and has developed valuable principles and procedures in both experimental and applied areas. However, in our effort to avoid inferred processes, we have sometimes neglected important phenomena, such as revaluation and blocking, that challenge analysis at the behavioral level.

Through the synthesis of behavior analysis with an increasingly rich neuroscience, we can achieve a more comprehensive understanding of a greater range of phenomena while remaining committed to a science that is grounded in experimental analysis (cf. Balleine & Dickinson, 1998). The treatment of revaluation presented here illustrates the promise of a biobehavioral approach: Revaluation phenomena arise as emergent products of fundamental biobehavioral processes. These processes accommodate a considerable range of findings while avoiding several counterfactual predictions of associationism. Finally, integrating behavior analysis and neuroscience does not compromise the independence of behavior analysis. As Skinner noted, drawing upon neuroscience to fill the "temporal gaps" between the environment and behavior "completes the account; it does not give a different account of the same thing" (Skinner, 1953, p. 18).

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